

DIOECY IN NORTH AMERICAN CACTACEAE: A REVIEW

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ABSTRACT

Of the six species of Cactaceae described as dioecious, only *Opuntia stenopetala* Engelm., *O. grandis* Pfeiffer and *O. glaucescens* Salm-Dyck are dioecious. *Mammillaria dioica* K. Brandegee and *M. neopalmeri* Craig are gynodioecious or possibly trioecious, differing from one population to another. *Selenicereus innesii* Kimmach is gynodioecious or probably hermaphroditic with sterile, abortive flowers that appear pistillate. Inadequate data and careless word usages have obscured the true sexual condition of the latter three species.

The sexual condition of the Cactaceae is generally regarded as being hermaphroditic, or monoclinal (Core 1955; Porter 1959): that is, all plants bearing perfect flowers (Swartz 1971). That there are exceptions is indicated by the Britton and Rose (1937) description of the family: "Flowers usually perfect . . ." Likewise, Bravo-Hollis (1978) in her description of the order Cactales hints that exceptions exist: "Flores . . . casi siempre hermafroditas . . ." Benson (1969a, 1969b, 1969c, 1982), in his description of the family avoids the issue.

To pursue the statement of Britton and Rose (1937), one must scan their 1235 species descriptions, for no mention of imperfect flowers is made at the generic level. One finds that three Mexican species of *Opuntia*, series *Stenopetalae*, and one primarily Mexican species of *Mammillaria* (as *Neomammillaria*) are considered dioecious.

Recently a new species from St. Vincent Island, West Indies, *Selenicereus innesii* Kimmach, was described as "the only confirmed example of complete dioecy (sic) in the Cactaceae" (Kimmach 1982).

TERMINOLOGY

Before examining these claims of dioecy (= dioecism, cf. Bawa & Opler 1975) in the Cactaceae one must first establish an understanding of the terminology. The usual sexual condition in cacti is *hermaphroditic* or *monoclinal*. This means that all plants of a given taxon have perfect (bi-sexual) flowers (Usher 1966; Swartz 1971, Radford et al. 1974). In contrast to hermaphroditic is *monoecious*: plants with flowers not perfect, the

staminate and pistillate flowers on the same individual. *Dioecious* plants also have all flowers imperfect (unisexual) but with the staminate and pistillate flowers on separate individuals (Radford et al. 1974). *Gynodioecious* seems to be transitional between hermaphroditic and dioecious (Ross 1970) with some plants bearing perfect flowers and others pistillate ones. The uncommon term, *trioecious*, refers to a species with some plants staminate, some pistillate, and some perfect (Jackson 1928, p. 392; Usher 1966; Swartz 1971; Radford et al. 1974, p. 144):

Although some authors describe individual flowers (rather than whole plants) as dioecious (Britton & Rose 1937; Kimnach 1982) or monoecious (Standley 1920–1926), in modern usage these words correctly may be used only to describe the arrangement of reproductive parts on whole plants (Lawrence 1951). Hence one may call a single flower staminate, pistillate or perfect, but before one may use the words defined in the preceding paragraph, one must know the sexual condition of other individual plants of the species (Lawrence 1951).

DISCUSSION

The pistillate flowers of *Selenicereus innesii* are described as lacking stamens and staminal nectaries, and as often having a reduced number of ovules (Kinnach 1982). The stamen-bearing flowers have nectaries, more numerous ovules, and a "style ca 4–5 cm long, ca 1 mm thick, the apical portion magenta, white below, the stigma lobes 7–8, lobate, obtuse, slightly expanding, 1–1.5 mm long and to 1 mm wide near apex." (Kinnach 1982). Kinnach refers to these as "perfect flowers."

It is clear from the description and illustrations (Kinnach 1982) that *S. innesii* is gynodioecious with pistillate and perfect flowers but no staminate ones. Therefore, this cannot be considered a species with "complete dioecy."

Of interest is the description of the ovule chamber in the flowers of the pistillate plant: "much of the cavity being occupied by one or more rudimentary styles terminating in stigmatic papillae." This, combined with the fact that the fruits and seeds are unknown, suggests that the structurally pistillate flowers may actually be malformed to the point of being totally sterile. If this proves to be the case and only the perfect flowers are functional, the species is neither dioecious nor gynodioecious but functionally hermaphroditic.

Mammillaria dioica K. Brandege is one of the four species considered by Britton and Rose (1937) as dioecious. However, they say it is "incompletely dioecious." When the species was originally described,

Brandegee (1897) stated that "Both the type and the variety (*insularis*) are nearly dioecious, many plants male, with imperfect, less-divided style-branches, which rarely bear fruit, and the few which occasionally appear (are) very slender and few-seeded; many female, with entirely abortive anthers and very small flowers, which usually produce a row of thick oval or clavate, coral berries; others hermaphrodite or imperfectly dioecious in all degrees." Lindsay (1967) commented that the *M. dioica* segregate, *M. engelensis* Craig, also has "occasional pseudo-dioecious flowers." Of *M. dioica*, Benson (1969b) states "plant with a strong tendency to be dioecious, i.e., for the flowers of some plants to have small, sterile anthers and large stigmas and those of other plants the opposite." In their discussion of *M. dioica*, Lindsay and Dawson (1952) state that dioecy represents "an exceptional rather than a usual character of the plant. The dioecious condition is not frequently observed, and moreover, is not confined to *M. dioica* but occurs occasionally in other species such as *M. neopalmeri*." Brandegee (1897) discussed *M. neopalmeri* (as *M. dioica* var. *insularis* K. Brandegee) with *M. dioica*, stating that flower parts are the same in both taxa (see above quotation from Brandegee).

A population of *M. dioica* was examined by Ganders and Kennedy (1978). They found some plants with perfect flowers and others with pistillate flowers. Both set fruit with apparently normal seed. No "male" flowers were seen. The pistillate flowers bore "stamens with indehiscent anthers that contain no pollen" (Ganders & Kennedy 1978). In a microscopic examination of the flowers of *M. dioica* and its segregates, *M. estebanensis* Lindsay, and *M. multidigitata* Lindsay, Bemis et al. (1972) determined that the functionally pistillate, "male sterile," flowers have indehiscent anthers with malformed pollen. Ganders and Kennedy correctly state that a (functionally) gynodioecious condition is indicated. However, they point out that they (Ganders and Kennedy) studied only one inland population, and that coastal plants observed by Brandegee (1897) may have been misinterpreted or may actually have had a different sexual condition. If the plants are as described by Brandegee (1897) and as indicated by Lindsay and Dawson (1952), the term trioecious would most accurately describe *M. dioica* and *M. neopalmeri*.

The description of *Opuntia* series *Stenopetalae* (Britton & Rose 1937) states "This is an anomalous group in *Opuntia* since the flowers are dioecious and the petals are linear and more or less erect." *Opuntia stenopetala* Engelm. is described as having "male flowers with an abortive, pointed style, but female flowers with 8 or 9 yellow stigma lobes on style . . ." *Opuntia grandis* Pfeiffer and *O. glaucescens* Salm-Dyck, the other two species of the series, are not described in comparable detail; no further mention is

made of dioecy in *Opuntia* in Britton and Rose (1937).

Bravo-Hollis (1978) supports the observations of Britton and Rose (1937) in her description of the genus *Opuntia*: "Flores generalmente hermafroditas . . ." Her key separates subgenus *Stenopuntia* from subgenus *Opuntia* on the basis of plants "unisexual" versus hermaphroditic, respectively. The "unisexual" character is repeated in the descriptions of the subgenus *Stenopuntia*, of *Opuntia stenopetala* and of var. *stenopetala*. The latter description is the most detailed: "estilo abortado en las flores masculinas, en las femeninas es muy grueso en la parte media; lóbulos del estigma 8 a 9, amarillos . . ." A population of this variety from el Cardonal, Hidalgo, Mexico, is described thus: "En las flores masculinas el gineceo está parcialmente atrofiado y el estilo es claviforme, abajo rosa y arriba amarillento con los lóbulos del estigma atrofiados pues terminan en una punta aguda, rígida; el ovario también atrofiado" (Bravo-Hollis 1978). The pistillate flowers are not described. *Opuntia stenopetala* var. *inermis* Bravo has similar flowers and *O. glaucescens* is "generalmente dioica" (Bravo-Hollis 1978). Although Bravo-Hollis' description of *O. grandis* does not mention dioecy, the species is in the subgenus characterized as "unisexual."

I examined the flowers of *O. stenopetala* on herbarium specimens at ASU. Seven of the eight sheets from different localities had only staminate flowers, a disproportionate number resulting from collection for meiotic chromosome studies (Pinkava, pers. comm.). Present with the stamens was a pointed style which lacked a stigma (Fig. 1).¹ Ovules were apparently lacking in the reduced ovule chamber in the staminate flowers of all but one specimen. The eighth sheet had flowers with style, stigma, and stamens (Fig. 2), but when the mature stamens were examined at 400x magnification, they were found to be indehiscent and completely lacking pollen. Thus, as in *Mammillaria dioica*, the flowers of the specimen appear perfect but are functionally pistillate. Because this small sample supports the previously published descriptions of the species, *O. stenopetala* is to be considered functionally dioecious. *Opuntia grandis* and *O. glaucescens* were not available for me to study. However, we might cautiously assume that they are also dioecious because according to both Bravo-Hollis (1978) and Britton and Rose (1937) the three species constitute a series or subgenus characterized by unisexual flowers.

CONCLUSIONS

Only six species of Cactaceae have been described as dioecious. Of these only *Opuntia stenopetala* is almost certainly dioecious. *Opuntia grandis* and *O.*

¹For illustrated longitudinal sections of the flowers of *M. dioica* and *S. imesii*, see Ganders & Kennedy (1978) and Kimnach (1982), respectively.

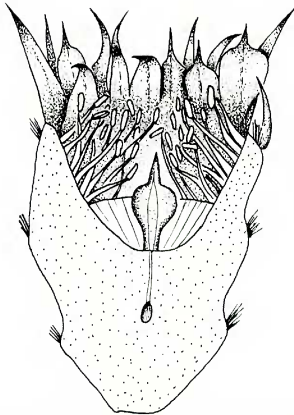


Figure 1. Staminate flower of *Opuntia stenopetala* in longitudinal section. Scale line equal to 1 cm.

glaucescens are probably dioecious also. *Mammillaria dioica* and *M. neopalmeri* are gynodioecious or possibly trioecious, apparently differing from one population to the next. *Selenicereus innesii* is gynodioecious or possibly hermaphroditic with sterile, abortive flowers that appear pistillate.

The sexual conditions of these cacti have been misunderstood for two reasons. First, inadequate data for the populations make it difficult to accurately assess the sexual condition of the species. Second, careless usage of the word dioecious has usually obscured the true sexual condition even where populations or species were studied adequately.

According to Brandegee (1897), other species, presumably of *Mammillaria*, are "completely unisexual." Doubtless there are species, in addition to those discussed here, in which the arrangements of reproductive parts need to be carefully observed and accurately reported.

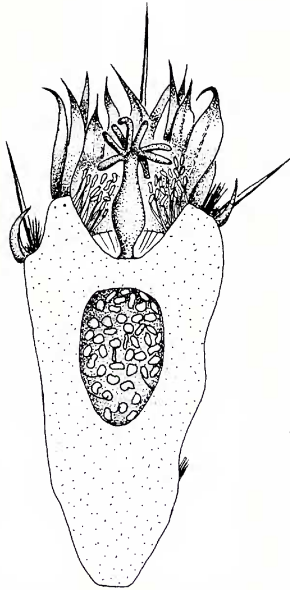


Figure 2. Functionally pistillate flower of *Opuntia stenopetala* in longitudinal section; the stamens produce no pollen. Scale line equal to 1 cm.

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